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Resistance of hosts and endoparasites; parasitological groups of hosts and types of systems „host—parasite"

Oporność żywicieli i endopasożytów; grupy parazytologiczne żywicieli a typy układów „żywiciel — pasożyt"

The explanation of the nature of the resistance of hosts and endoparasites, the determination of criteria on the basis of which it would be possible to characterize the various types of systems „host-parasite" occurring in the Nature and to study their variability, may be not only of practical value (elaboration of proper methods of control of endoparasites, biological methods included), but may play also an important role in general biology. The evolution of parasites and the phylogenesis of their hosts are often more or less closely and permanently bound together. Resistance and other phenomena, which occur as a result of the nature of this relationship often characterize it very accurately.

The system „host-parasite", as a specific biological entity can be the object of the action of natural selection. Under such specific conditions the studies of the system may reveal extremely interesting biological data.

The following notes deal mainly with systems formed by the larvae of tapeworms and their first intermediate hosts — *Copepoda*.

I. Factor conditioning the formation of systems „host—parasite"

Pavlovskij (1946) differentiates three fundamental factors, which play a decisive role in the formation of systems „host — parasite". Predestinating factors depend on the anatomical and

physiological features of the organisms, which enter into a relation, fixative factors are linked with their biocoentotic connections, finally exogenic factors secure the survival of a virulent parasite in the organism of a host. Šulc and Davtian (1954) differentiate only two categories of factors — admitting factors, which depend on the organisms of hosts and parasites, and realizing factors, that is factors of the external environment. Refraining from analysis and evaluation of such presentations I should like to stress, that in view of the character of the theme, in which we are interested, it would be purposeful to deal briefly with factors of the external environment, which condition the formation of the systems. Next I should like to draw closer attention first on the factors dependent on the organism of the host — and subsequently — on the parasite.

A. Environmental factors of the second order

Conditions of the external environment, that is geographical, ecological and phenological conditions can exert an important influence on the formation of systems „host-parasite", because of the common geographical and ecological zones of their occurrence, presence of suitable alimentary chains, synchronization of their occurrence and so on. They can most likely exert also other, hitherto unknowa influences. This is evidenced even by data which are an indication of the separateness of the role played by the same species of hosts towards the same species of parasites under different geographical conditions. A major role can be played also by the influence of an environment of the second order on the free developmental forms of parasites temporarily living in it. It is enough to mention that, e.g., light may be a decisive factor for the hatching of larvae of some tapeworms from eggs (Dubinina, 1957), temperature of water — for fluctuations of the invasiveness of larvae hatched from eggs of *Diphyllobothrium latum* developing in it (Guttowa, 1955), length of time the eggs of *Drepanidotaenia lanceolata* stay in water before they become devoured by cyclops — for the course of the development of cercocysts of this tapeworm in their body cavity (Kisielewska, 1957). I am not intending to deal closer with these prenomena, especially not with the last of them, which has a character of an adjourned influence on the system through the organism of the parasite. Here we should stress, that it would be difficult to classify them to any category of factors, differentiated by the cited authors.

B. Environmental factors of the first order (organism of the host)

Studying the conditionings of systems by factors depending on the host there should be differentiated among them above all the biological factors (e.g. season of the occurrence in the course of a year, kind of food) and etological factors (behaviour in various seasons of the year and various parts of the day, way of prehension of food). They decide on the possibility of a contact between the partners of a system and on the eventual entering into closer relation. All other factors, which come into play under conditions of the existence of this contact should be determined by the general term resistance (resistentio, soprotivlaemost'). This very broad term resistance would, therefore, include several phenomena deserving attention.

1. Mechanical resistance

To this category of phenomena should be included all the characteristics of the morphological structure of the host which are to the parasite inhibiting in the gaining by him suitable for him microbiotops of his body. To such belong, e.g., thickness of the skin of the host, or its structure, thickness of the gastric wall (which, e.g., according to Pavlovskij and Gnezdilov, 1939 make it impossible to invade old turtles with plerocercoids of *Diphyllobothrium latum* while young turtles become invaded). Of course, the formation of mechanical resistance of the host under the influence of parasitism cannot be totally excluded, but this form of resistance seems very little likely to occur and probably most commonly it is of a secondary character, or altogether accidental.

2. Physiological resistance

To this category of phenomena belong physiological properties of the host which are not a direct, actual reaction of an individual to a parasitic invasion. They need not necessarily be a model of a reaction formed in the course of evolution.

The invasion of parasites may be influenced, e. g., by the temperature of the host. Occording to Matoff (1944) the larvae of *Trichinella spiralis* can at the temperature 35° C gain access to such unusual to this species hosts, as frogs and salamanders.

Undoubtedly the composition of the gastric juices of the various hosts plays an important role. E.g., it is well known that *Cladocera*

digest an enormous majority of the swallowed larvae of the various species of tapeworms, while *Copepoda* digest some of them, but succumb to others. Most likely, we are most commonly dealing in such cases with an accidental natural resistance. Although it would be impossible to exclude completely the existence of resistance of this type acquired in the course of evolution, nevertheless it would be difficult to imagine a mechanism of selection based on this characteristic, because, e. g., *Copepoda* even intensily invaded with larvae of some parasites, most frequently do not die as a consequence of such an invasion.

To the same category of phenomena we can include the known facts that parasites fail to develop in the intestine or body cavity of an improper, or accidentally invaded host, because of the disagreement of conditions reigning there with their vital requirements (e.g., lack of resorptive food components). Of course, it is difficult to state always, whether we are dealing only with such physiological disagreement, or with an immunological influence of the host (may be even evolutionally acquired). However, the fact that an inhibition, or even a complete arrest of the development of parasites in hosts of small immunological influence was observed (e.g. *Copepoda*) confirms the fact of the existence of an unspecific, physiological resistance of this type.

3. Incystation and isolation of parasites

The known cases of incystation and isolation of parasites which take place in the host, who makes use of his tissues and humoral factors, constitute a category of resistance, causatively connected with the invasion of the parasites and certainly is of evolutionally moulded tendencies. To the same category can be included cases of parasitological autotomy.

4. Immunity

Immunity (immunitio) should be treated as a particular property of hosts and it is one of the elements of the complex of the phenomena of resistance. It is a set of humoral reactions, which oppose the invasion of parasites, or their effects.

Among the previously characterized categories of phenomena of resistance, there occur both a c c i d e n t a l (e. g., accidental mor-

phological or physiological disagreement, or agreement of hosts and potential parasites) and adaptive phenomena. The latter ones were formed as a result of the influence of natural selection in consequence of mutual contacts of hosts with definite parasites. To every one of the categories can be classified both the natural resistance (primary) and the acquired one (secondary), resistance linked with age, sex, intensity of invasion and them like. The immunity of hosts to parasitic invasions corresponds fundamentally to the analogous phenomena, which accompany infectious diseases (Šichobalova, 1956). There are considerable differences of opinions as regards the presentation of the mechanism of immunity, its nature, classification of the various kinds of immunity (natural and acquired, species and individual resistance — Dogiel, 1947; primary and secondary resistance — Šulc and Bondareva, 1955 etc.).

From the point of view of the evolutional formation of systems „host-parasite" we can differentiate accidental immunity (accidental or biochemically unfavourable, active instanteneously or adjourned humoral influence of the host on the parasite) and adaptive immunity. Adaptive immunity includes evolutionally conditioned immunological reactions of the host.

Inborn immunity does not depend on the previous contact with the parasite. Acquired immunity, occurring in the separate individuals after a shorter or longer contact with the parasite, is conditioned by previous contacts in the course of phylogenesis and is transmitted in a hereditary way. The differentiating of accidental and adaptive immunity and — as regards the latter one — inborn and acquired ones — is not easy and requires a number of other data referring both to the host and to the parasite to be taken into consideration. From the evolutional point of view the variability of the adaptive immunity draws attention. This variability, as proved by numerous data in the literature, can be connected with the race (e. g., Šulc and Bondareva, 1955), condition, age (e.g., Dogiel, 1947, Chabaud, 1957), sex (e.g., Michajłow, 1932, Šichobalova, 1950), influence of the nervous system of the host (e.g., Šulc and Andreeva, 1954), composition of its food (e.g., Šichobalova, 1950, Chabaud, 1957), intensity of the invasion of parasites (e.g., Pocelueva, 1955, Paruchin, 1954) and other factors.

C. Factors depending on the parasite

The problem of the resistance of parasites to the host received, as hitherto, not much attention, although, e. g., the problem of the specificity of parasites occupies in the parasitological literature a lot of space. The relation between the hosts and parasites was from the parasites' aspect discussed by Becker (1953). Considering the phenomena of the resistance of parasites to the influences of the organism of the host, we are able to discern categories similar to those differentiated in referring to hosts. We are dealing with mechanical resistance of parasites when, e.g., the coracidia of *Pseudophyllidea,* loose in the course of being swallowed by *Copepoda* only the ciliated cover, or during their passage through the intestinal walls — the second larval cover, whereby the oncosphere remains always uninjured. The specific physiological resistance of those larvae depends on that they resist efficiently to the action of digestive juices of some *Copepoda,* but succumb to the action in other species. As regards those and them like examples of morpho-physiological resistance of parasites we are in a position to speak also of accidental properties, or elaborated and formed evolutionally due to continuous contacts with potential hosts.

Immunity of parasites to hosts is manifested above all by their more or less efficient defence against the action of enzymes, antibiotics, proteins and products of their disintegration, phagocytes and protective humoral reactions of the hosts (Becker, 1953). Although among the investigators of the antigenic and buffer properties of parasites the opinion is not uniform as regards the time of the evolutional formation of those substances (before changing to parasitism or in the course of the passage) their role in the historical formation of the systems „host-parasite" cannot be doubted.

To the problem of the formation of systems and their value, of importance is the question of the routes of the invasion of the parasite and the mode of its localization in the organism of the host. In respect to endoparasites we can discern (1) the alimentary route, which leads to the alimentary tract of the host (lumen of the intestines, their walls), to the circulatory system (blood, lymph), to the body cavity and internal organs, (2) the route, which leads through the body cover to the circulatory system, body cavity and internal organs, and finally — (3) direct passage to the blood of the host by the assistance of arthropods. From the point of view of the forma-

tion of systems it is important that the parasite has to conquer only one selective barier (e.g., remaining in the intestine after reaching it by the alimentary route, or by direct passage to the blood of the host), or two such bariers (in all other cases, e.g., in the course of passing the intestinal wall, in the course of gaining internal organs after the penetration of the skin).

All the above mentioned phenomena are correlated with the problem of the specificity of the parasites towards their hosts. This problem cannot be here discussed freely, though it is impossible to omit it altogether.

Among the definitions of the specificity of endoparasites most apt is the one proposed bu Šulc and Davtian (1955), namely: „The specificity of hosts and parasites is a relative morpho-physiological adaption of a parasite to the given host (or to several hosts). This adaptation depends on (1) the agreement of requirements of the parasite with the conditions of its existence in the given host, (2) on the ability of the parasite to overcome in a definite degree the defence mechanisms, which the host presents as the opposing measures". As evident, specificity includes both the phenomena of resistance and immunity of the hosts and parasites. Of course, by this we understand species specificity (infraspecificity Hargis, 1957), which is of the greatest importance from the point of view of the characteristic of the individual systems and the search of ways of their arising. It may, or may not be identical to topic specificity, which is a form of an adaptation of a parasite to live in definite organs of hosts. Species specificity plays a direct role in the maintenance and speciation of parasites. Specificity towards higher groups (supraspecificity, Hargis, 1957; vstrečaemost' of Russian authors), which among other themes was represented in manifold theoretical definitions in the form of the so called parasitogenetic rules, can be only defined on the basis of concrete studies of cases of species specificity and is in some way their resultant. It can serve only as an indication by the reproduction of the phylogenesis of parasites and hosts.

II. On parasitological groups of hosts

Already before the introduction and definition of the term specificity of parasites towards hosts it was known that certain parasites are able to infest only certain species of hosts. Among them, one become easily infested and are better hosts; other species — not as fre-

quently and to a lesser degree, therefore they are worse hosts. Finally, it was known that the resistance of the proper hosts to parasites is variable and subject to individual fluctuations. However, no many accurate studies were conducted on the evaluation of species of hosts from this point of view. Taking as a basis the resistance of hosts and specificity of parasites defined by the use of certain indicators (extensity and intensity of invasion, course of development in the body cavity) I made a subdivision (Michajłow, 1932) of a number of species of *Copepoda* — intermediate hosts of the tapeworm *Triaenophorus lucii* — into five parasitological groups (1 — V). The corresponding groups of *Copepoda* were differentiated in relation to another tapeworm — *Diphyllobotrium latum* (Michajłow and Wierzbicka, 1935). Methodical assumptions were precisely defined to secure that in similar studies comparative results could be obtained (Michajłow, 1938).

Applying the assumptions Humes (1950) classified *Copepoda* the first intermediate hosts of *D. latum* in the United States. In the same way Guttowa (1956) differentiated *Diaptomus vulgaris* as the main (or one of the main) intermediate host of *D. latum* for Poland, and established the belonging of other examined *Copepoda* to the corresponding groups. The works of Dubinina (1950) on *Ligula intestinalis* indicate that among the first hosts of this tapeworm the mentioned groups can be also differentiated (Michajłow, 1951).

The cited studies concerned tapeworms of the group *Pseudophyllidea*. Kisielewska (1955, 1959) proved that similar classification of hosts (*Copepoda*) can be made when dealing with the larvae of *Drepanidotaenia lanceolata*, a tapeworm belonging to *Cyclophyllidea*.

The above data referred to parasites living in the body cavity of hosts. The parasites had to overcome two selective barriers (the action of the intestinal contents and that of the body cavity of the host).

As regards *Astasia cyclopis* Michajłow, the representative of *Flagellata* (*Euglenida*), which lives for some time in the intestine of the host — cyclops, therefore has to conquer one selective barrier, the following groups of hosts, were established: I — the cyclops digest all the swallowed flagellate forms of the protozoa, II — intestinal juices destroy part of the parasites, but the extensity and intensity of the invasion are considerable, the development runs a normal course, III — intestinal juices do not act in a destroying way, the extensity and intensity of the invasion are very large, the deve-

lopment runs a normal course (Michajłow, 1957). The theoretical possibility of the existence of the IVth group, including hosts of large extensity and intensity of invasion, but with an inhibited, or otherwise deformed course of development of the parasites has not been up to now in this case experimentally confirmed.

It can be expected that the above described phenomena are considerably more common. This is proved, among others, by the frequent use in parasitology of terms not precisely accurate and not always synonymous such as auxiliary host, complementary, potential, accidental, vicarious and them like. The existence of various groups of hosts, however, can be revealed, provided that suitable and uniform investigative methods are employed.

It should be stressed that the previously mentioned authors, who differentiate parasitological groups of hosts drew attention to the lack of sharp borderlines between them, to the variability dominating within groups and to the dependence on the sex of the host (Michajłow, 1932; Kisielewska, 1959), its age (Michajłow, 1951; Guttowa, 1956) and to the influence of such factors, as the season of the year, in which the invasion takes place (Kisielewska, 1957, 1959) and ecological conditions (Michajłow, 1957). Closer investigations into the phenomena can, among others, contribute towards the elucidation of the problem of the evolutional formation and development of the systems „host-parasite".

III. On the types of systems „host-parasite"

The term of the system „host-parasite" denotes a set of organisms composed of two species; between them is established a specific biological connection, called parasitism. In the ideal case, when to one host corresponds only one parasite, we are dealing in some measure with a model of parasitism in its pure form. However in the Nature this happens extremely exceptionally, because usually the host is invaded with numerous specimens of one, or several species of parasites, which form a complex parasitocoenosis. In such a case we are dealing most commonly with a summation of the action of the whole parasitocoenosis on the host and its reaction to this complex action. We are able to abstract the relations of the simple system (two species and two individuals) from this complex set of reactions. In spite of the difficulties the introduction of the term of the system „host-parasite" is useful and purposeful, because it enables to treat as a wholeness a complex set of phenomena of resistance of hosts and pa-

rasites. Besides, it seems very likely that to the influence of natural selection are exposed not only the hosts and parasites in the various stages of their life, but also the system as a wholeness, on the fate of which depends to a considerable degree the fate of its components (in a major degree — that of the parasites, in a lesser, but nevertheless not in a small degree — that of the hosts). The vitality of the term of the system is proved among others by the attempt to introduce a classification of the systems „host-parasite".

Accepting as a basis the physiological criteria (specificity of parasites), ecological (factors which secure contact of hosts and parasites) and historical (phylogenetic), Šulc and Davtian (1954) differentiated four types of systems „host-parasite", namely: obligatory, facultative, abortive and captive. This classification is based on the evaluation of the degree of the mutual adaptation, on informations concerning the course of the development of the parasite (attainment of sexual maturity or a definite degree of the invasiveness of parasites), and on the analysis of the evolutional connections of both links in the past. Between some of types of Šulc and Davtian's systems and the „parasitological groups" of hosts a convergence can be easily observed. And so, e.g., the obligatory system assumes the presence in its composition of main hosts (V group), the facultative system — auxiliary hosts (IV group). Against the classification of Šulc and Davtian the following reservations could be made. It is not based on distinct, statistically represented criteria of the extensity and intensity of invasions. It takes into consideration rather their general result in the form of immunity, what makes difficult the characterization of the variability within the systems of the given type. The phylogenetic criterion assumes previous obtaining of informations concerning hosts and parasites and the history of their system, and the latter one can be reproduced often not before an analysis of the relations in the system is performed. Finally, this classification, most probably intended to be universal, does not include all types of relations between hosts and parasites. And so, e.g., the classification does not include the relations between the procercoids of *Triaenophorus lucii* and their hosts, which belong to the IInd and IIIrd groups. Their resistance expressed by strong action of intestinal juices makes impossible to the larger part of the larvae an invasion, and the resistance of those larvae to the conditions prevailing in the body cavity of the host is smaller (IInd group(, or larger (IIIrd group).

It seems that the problem of a synthetic presentation of all types of systems „host-parasite", especially such one which would be connected with the problems of evolution, is not yet mature. The way to synthesis in the sphere of the typology of systems „host-parasite" must lead through a detailed analysis of concrete data referring to various endoparasites. Into consideration must be taken the extensity and intensity of invasion, its routes and course, ways of conquerring selective barriers, effects of invasion on the host, course of the development of the parasite and the influence of the environment of the second order. This way should lead through an analysis of the corresponding relations which take place in the definite groups of hosts and parasites.

Because the relations in the systems depend to a major degree both on the host and on parasites it seems desirable that a systematic elaboration of the systems composed of compact groups of endoparasites and their hosts is required. Drawing the attention to systematic groups of hosts, e.g., to: *Gastropoda* and *Ciliata*, which parasitize in them, *Gastropoda* and *Trematoda, Gastropoda* and *Nematoda, Copepoda* and larvae of *Cestoda, Copepoda* and *Flagellata, Ostracoda* and larvae of tapeworms, *Pisces* and plerocercoids of tapeworms, birds and mature tapeworms, has this advantage that in case of phylogenetic specificity (not ecological) we collect many data on the systems, their specificity etc., therefore also we gain informations as regards factors which condition their evolution. Considering the same from the side of the parasite (e.g., tapeworms of a definite group which parasitize in hosts belonging to various groups) may contribute towards the analysis of their specificity, especially to the ecological specificity, and may throw light on factors causing variability of the parasites and their phylogenesis.

It seems, that within systems composed of *Copepoda* as the hosts of larvae of various tapeworms we can already at present make a classification of the systems „host-parasite".

Such an attempt was undertaken by Kisielewska (1959) with the application to *Copepoda* and the larvae (cercocysts) of the tapeworm *Drepanidotaenia lanceolata*. The classification proposed by her is as follows: (1) Proper system (systema obligatorium) is characterized by maximal extensity and intensity of invasion (the first selective barrier is conquerred by the parasite easily) and by normal course of development of the parasite; (2) Auxiliary system (s. auxiliare) — of smaller extensity and intensity of invasion (the obstacle

in the gaining of the host is the first selective barrier) but normal course of development; (3) Accidental system (s. accidentale) — of small extensity and intensity of invasion and most commonly of an inhibited development of the parasite (both selective barriers impede here the gaining of the host); (4) Spurious system (s. spurium) — faint extensity and intensity of invasion, development completely inhibited, therefore the main role is played by the second selective barrier.

This classification takes into consideration the phenomena of resistance and immunity, the existence of two selective barriers, makes possible exact registration of the variability of the systems. It is partly in agreement with the subdivision of hosts into groups (the proper system includes the Vth group of hosts, the auxiliary — the IVth, the spurious — the II nd). Objections could be raised to the purposefulness of the differentiating of the spurious system, which does not secure development even to a part of the parasites, therefore it actually does not play any role. However, taking into consideration the variability of the systems we cannot be certain that a spurious system does not change after some time into another one, e.g., into accidental, or whether already at present under certain conditions such a change is not taking place. Registration of spurious systems is purposeful also because undoubtedly many species, put some time ago on the list of hosts as a result of the observation of the sole presence of parasites at any stage of their development, will require a classification as constituents of such exactly spurious systems.

It should be born in mind, that the proper system can be composed not only of main hosts. If we define as such ones hosts which play the main role in a given biotope, than it may happen that systems differentiated on the basis of experimental studies, where the physiological criterion prevails, as the proper, will not necessarily play the main role under definite ecological conditions (K i s i e l e w s k a, 1959). The mentioned types of systems differentiated in relation to *Copepoda* and *Drepanidotaenia lanceolata* can be applied to *Triaenophorus lucii, Diphyllobothrium latum* therefore, most probably to all larvae of tapeworms which parasitize in their body cavity. Presently this concept should be extended to larval forms of other species of tapeworms and hosts of the group *Copepoda,* and should be confronted also with the data referring to other larval forms and mature tapeworms and other intermediate and final hosts.

Table I

„Astasia cyclopis Michajłow — *Copepoda"**

Protozoa
Flagellata
Euglenida

Copepoda

Clay-pits from environments of Warsaw

Systema obligatorium	Systema auxiliare	Systema accidentale	Systema spurium
1. *Eucyclops serrulatus* (Fischer); ♀♀,♂♂: IX, X, XI, XII,I; Nat.: E — 82%, I — 11.3 (1 — 27); Exp.: E — 100%, I — 13.5 (1 — 45); 2. *Eucyclops macruroides* (Lill.); ♀♀, ♂♂: IX,X,XI,XII,I; Nat.: E — 50%, I — 5 (2 — 10); Exp.: E — 100%, I — 19.2 (2 — 80). 3. *Eucyclops macrurus* (Sars); ♀♀, ♂♂: IX,X,XI,XII,I; Exp.: E — 100%, I — 27 (4 — 99).	1. *Macrocyclops albidus* (Jur.); ♀♀, ♂♂: IX, X, XI, XII, I; Exp.: E—6%, I —3.5 (2—6) 2. *Acanthocyclops viridis* (Jur.) ♀♀, ♂♂: IX,X,XI,XII,I; Nat.: E — 36%, I — 3.5 (2 — 6); Exp.: E — 37%, I — 3.7 (1 — 6). 3. *Cyclops vicinus* Ulj.; ♀♀, ♂♂: IX,X,XI,XII,I; Exp.: E — 50%, I — 4 (1 — 12). 4. *Cyclops furcifer* Claus; ♀♀, ♂♂: IX,X,XI,XII,I; Exp.: E — 30%, I — 22 (15 — 26). 5. *Cyclops insignis* Claus; ♀♀, ♂♂: IX,X,XI,XII,I; Exp.: E — 27%, I — 15 (1 — 48). 6. *Cyclops s. strenuus* Fischer; ♀♀, ♂♂: IX,X,XI,XII,I; Nat.: E — 30%, I — 3 (3 — 5); Exp.: E — 43%, I — 9.5 (1 — 37).	Not noted	Absent

Not invadible: *Diaptomus gracilis* Sars, *Diaptomus vulgaris* Schmeil, *Macrocyclos fuscus* (Jur.), *Mesocyclops leuckarti* (Claus).

* After Michajłow 1957; Exp. — experimental, Nat. — natural invasion; E — extensity, I — intensity of invasion.

The possibility to apply such a classification of the systems also to other groups of parasites is proved by the data referring to *Astasia cyclopis* (*Flagellata*) and their hosts — *Copepoda*. In this case we are dealing with one selective barrier (M i c h a j ł o w, 1957) and the following types of systems can be differentiated: (1) The proper system (*A. cyclopis — Eucyclops serrulatus, E. macruroides, E. macrurus*) (2) The auxiliary system (*A. cyclopis — Macrocyclops albidus, Acanthocyclops viridis, Cyclops vicinus, C. furcifer, C. insignis, C. strenuus*). The theoretically possible accidental system has not been hitherto found (Table I).

The lack of sharp borderlines between systems, and their variability, dependent on the properties of the individual hosts and parasites, on the intensity of the invasion, as well as on ecological and phenological factors, indicate that the systems as specific biological units, can undergo development along definite lines. Making a classification of systems we have to take into consideration the known fact of their not uniform value in the various geographical regions (G u t t o w a, 1957).

Among others, exactly this variability of systems enforces the use of accurate methods of their investigation in order to achieve comparable results.

IV. On the requirement to use uniform methods of investigations of the systems

The use of an uniform method should concern both field studies and experimental investigations, whereby the two ways of investigations should supplement each other. In field studies, besides the requirement to collect a sufficient, statistically essential number of observations, the following data should be also obtained: (1) Geographical situation of the locality; (2) Ecological characteristic of the terrain; (3) Accurately diagnosed species of host, eventually even its variety, race, subspecies; (4) Sex of the host; (5) Its age; (6) General notes on its condition and behaviour; (7) Accurate name of the parasite (in case the name is difficult to establish, e.g., as with some larvae — a description, eventual a drawing); (8) Developmental form of the parasite; (9) Date of the observation; (10) Extensity of the invasion; (11) Mean intensity of the invasion; (12) Its limit and most frequently occurring values; (13) Presence of other parasites in the host.

The tabular arrangements of the data for a given terrain should include accurate names of both species which take part in the system,

dates of observations, sex and age of the host, data on the developmental forms of the parasite, extensity and intensity of the invasion and its fluctuations.

In experimental studies it is indispensable to respect certain conditions. In all cultures intended to be mutually compared uniform conditions (e. g., temperature, light, thickness of the layer of water) must be preserved. The experiments should be conducted at least through the whole period of the occurrence of the host and parasite under natural conditions. It is desirable to use in the individual preliminary cultures and in experiments the progeny of parasites originating from the same specimen of the host, even better — of the same parental individual (e. g., segments of the same tapeworm) in order to take into account the moment of inheritance and individual variability. Into consideration should be also taken the influence of the factors of the free environment of an adjourned action (e. g., influence of low temperature on eggs and larvae of some tapeworms, G u t t o w a, 1956; their prolonged abiding in water in others, K i s i e l e w s k a, 1956).

The material must be invasive, and its invasiveness must be confirmed on an established main host (control), in whom the index of invasiveness is close to 100 (G u t t o w a, 1955).

The methods of observation of the course of development can be either statistical (studies on the state of the definite number of parasites in the observed, or periodically killed hosts, and tabular arrangement of the data), or they can be based on individual cultures of hosts (of translucent cover of the body), and on repeated observations of the same parasites in the course of their development (M i c h a j ł o w, 1953).

As a result of the comparison of the field and experimental data we should receive: (1) A list of species occurring in a given biocoenosis which are in direct touch with the parasite, but do not succumb to the invasion (Ist group). The necessity to establish such lists is motivated by the possibility of the occurrence of potential hosts, hosts replaced in other regions by other species (parasitological vicariate), etc. (2) List of hosts with their subdivision into groups (II — V), or, as far as natural conditions are concerned — establishment of main and auxiliary hosts. (3) Classification table of systems „host-parasite" subdivided into the previously mentioned types in which the constant element will be the species of the parasite, the variable — the host. This table should show the data which condition the even-

Table

Cestoda *"Drepanidotaenia lanceolata*
Cyclophyllidea experimen

Systema obligatorium	Systema auxiliare
1. *Cyclops s. strenuus* Fischer, ♀♀: III, IV, V, — E — 100%, I — 19.7 (7 — 32); VI, VII, VIII, — E —100%, I — 22.8 (12 — 45); ♂♂: III, IV, V, — E — 100%, I — 21.2 (3 — 51); VI, VII, VIII, — E — 100%, I — 18.1 (9 — 22); Cop. IV, V: III, IV, V, — E—100%, I — 16.3 (2 — 21); VI, VII, VIII, — E — 100%, I — 20.8 (6 — 38).	1. *Macrocyclops albidus* (Jurine), Cop.: IX, X, XI, — E — 100%, I — 6.9 (2 — 14); XII, I, II, — E < 100%, I — 6.1 (4—9)
2. *Mesocyclops leuckarti* Claus, ♀♀: III, IV, V, — E — 93,5%, I — 13.8 (9 — 12); VI, VII, VIII, — E — 100%, I — 10 (8 — 17).	2. *Mesocyclops leuckarti* Claus, ♀♀: XII, I, II, — E <100%, I — 9.2 (4 — 16).
3. *Acanthocyclops bicuspidatus* (Claus), ♀♀: III, IV, V, — E — 100%, I — 13.3 (12 — 19) VI, VII, VIII, — E — 100%, I — 16.8 (11 — 22).	3. *Acanthocyclops bicuspidatus* (Claus), ♀♀: XII, I, II, — E < 100%, I—5.8 (4 — 9).
4. *Acanthocyclops viridis* Jurine, ♂♂: III, IV, V, — E — 100%, I — 10.2 (2 — 29), VI, VII, VIII, — E — 86,3%, I — 6.6 (3 — 10). Cop.: VI, VII, VIII, — E — 100%, I — 12.7 (11 — 16).	4. *Eucyclops macrurus* Sars, ♀♀: III, IV, V, — E — 37.4%, I — 4.5 (1 — 8). 5. *Acanthocyclops viridis* Jurine, ♀♀: VI, VII, VIII, — E — 41.9%, I — 3.4 (1 — 7) 6. *Cyclops s. strenuus* Fischer, Cop.: VI, VII, VIII, — E — 100%, I — 4.8 (1 — 16)

* After Kisielewska, 1959. Explanations as in Table I.

II

Bloch (cercocyst) — *Copepoda*"* *Copepoda*

tal data Bodies of water from environment of Warsaw

Systema accidentale	Systema spurium
1. *Cyclops s. strenuus* Fischer, ♀♀: IX,X,XI,—E—100%, I—8.1(3—14), XII,I,II,—E—56.3%, I—9.4(2—15), ♂♂: IX,X,XI,—E—100%, I—7.4(2—16), XII,I,II,—E—100%, I—8.1(3—14). Cop.IV,V:—IX,X,XI,—E—62.3%, I—5.2(1—16), XII,I,II,—E—59.6%, I—11.3(12—15).	1. *Acanthocyclops viridis* Jurine, ♀♀: XII,I,II,—E—9.6%, I — 2.1 (1 — 6). 2. *Cyclops furcifer* Claus, ♀♀: III,IV,V,—E— single specimens, I—3.7 larvae degenerate.
2. *Macrocyclops fuscus* (Jurine), ♀♀: IX, X, XI,—E—100%, I—2.5 (2—3) XII,I,II,—E < 100%, I—1.7(1—2).	
3. *Macrocyclops albidus* (Jurine), ♀♀: IX,X,XI,—E<100%, I—4,8(1—10), XII,I,II,—E—12.1%, I—4.7(2—8), ♂♂: IX,X,XI,—E<100%, I—6.1(2—10), XII,I,II,—E—67.6%, I—5.8(1—12).	
4. *Acanthocyclops viridis* Jurine, ♀♀: IX,X,XI,—E—34,0%, I—3.2(1—8), III,IV,V,—E—87.1%, I—7.8(3—17), ♂♂: XII,I,II,—E—81.7%, I—5.2(1—14). Cop.: XII,I,II,—E<100%, I—1.4(1—2) III,IV,V,—E—90.9%,I—2.7(1—6)	
similarly:	
5. *Eucyclops macrurus* Sars,	
6. *Eucyclops macruroides* (Lill.),	
7. *Eucyclops serrulatus* s. str. Fischer,	
8. *Eucyclops speratus* (Lill.),	
9. *Cyclops vicinus* Ulj.,	
10. *Acanthocyclops vernalis* (Fischer)	

tual variability of the system (season of the year, sex, age of the host), which, depending on those data, may appear in several rubrics. If possible this table should include data on natural invasion and experimental invasion, properly marked (nat. and exp.).

To illustrate the proposed presentation I am enclosing as exemplary the table, which refers to the system *„Astasia cyclopis — Copepoda"* (Table I) and *„Drepanidotaenia lanceolata* (cercocysts) — *Copepoda"* (Table II).

Similar tabular arrangements concerning various biotopes and geographical regions can in the course of time become an interesting material for conclusions on the biology of parasites, zoogeography of hosts and zoogeography of parasites (parasitogeography).

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STRESZCZENIE

Celowe wydaje się wyróżnianie oporności (*resistentio*) jako całokształtu właściwości żywiciela utrudniających inwazję endopasożytów i ograniczających ujemne jej skutki, oraz odporności (*immunitio*), jako zespołu reakcji humoralnych natury immunologicznej. Oporność jako pojęcie zawsze obejmuje oprócz zjawisk odporności także czynniki morfologiczne wpływające na przebieg inwazji, gdy może ona dojść do skutku w określonej sytuacji ekologicznej. Z punktu widzenia ewolucji żywicieli wyróżnić można oporność przygodną (przypadkową niezgodność lub zgodność morfologiczną lub fizjologiczną żywicieli i potencjalnych pasożytów) oraz przystosowawczą, powstałą wskutek działania doboru naturalnego w toku stykania się żywicieli z określonymi pasożytami. Pod jedną z tych dwu kategorii podpadać może zarówno oporność naturalna (pierwotna), jak i nabyta (wtórna), oporność związana z wiekiem, płcią, intensywnością inwazji itp. Podobnie jak inne właściwości organizmów, oporność żywicieli wykazuje naturalną zmienność indywidualną oraz zmienność zależną od środowiska.

Pojęcia oporności i odporności (zarówno przygodnej jak i przystosowawczej) stosują się także do pasożytów. Indywidualna oraz zależna od czynników środowiska zmienność oporności odgrywa zapewne dużą rolę w ewolucji pasożytów.

Na podstawie oporności żywicieli i swoistości pasożytów dokonałem (Michajłow, 1932) podziału szeregu gatunków oczlików — żywicieli pośrednich larw *Triaenophorus lucii* (Müll.) na pięć grup parazytologicznych charakteryzujących się stopniem ekstensywności i intensywności inwazji oraz przebiegiem rozwoju pasożytów w jamie ciała żywicieli. Dane te potwierdzone zostały następnie w stosunku do *Copepoda* — żywicieli larw niektórych innych tasiemców (Michajłow i Wierzbicka, 1935, Humes, 1950, Dubinina, 1950, Kisielewska 1950, Guttowa, 1956). W stosunku do pasożytów jelitowych można na przykładzie *Astasia cyclopis* Michajłow wyróżnić następujące grupy oczlików: I — oczliki trawią wszystkie połknięte pierwotniaki, II — soki jelitowe niszczą część osobników, pozostałe przy zyciu rozwijają się normalnie, III — soki jelitowe nie działają niszcząco, rozwój pasożyta normalny (Michajłow, 1957).

W obrębie grup panuje zmienność uwarunkowana przez indywidualne właściwości żywiciela i pasożyta oraz czynniki środowiska.

Można więc mówić o ewolucji układów „żywiciel-pasożyt" jako pewnych jednostek biologicznych podlegających działaniu doboru naturalnego. Celowe wydaje się wyróżnianie określonych typów układów „żywiciel-pasożyt", przynajmniej w stosunku do endopasożytów i ich żywicieli. Droga do syntezy w zakresie typologii układów „żywiciel-pasożyt" prowadzić musi poprzez szczegółową analizę konkretnych danych dotyczących różnych endopasożytów z uwzględnieniem ekstensywności i intensywności inwazji, jej dróg i przebiegu, pokonywania barier selekcyjnych skutków dla żywiciela, przebiegu rozwoju pasożyta i wpływu nań środowiska drugiego rzędu. W stosunku do *Copepoda* i larw tasiemców wyróżnić można (K i s i e l e w s k a, 1959) 4 typy układów: 1) u. właściwy (maksymalna ekstensywność i intensywność inwazji, rozwój w jamie ciała normalny), 2) u. pomocniczy (mniejsza ekstensywność i intensywność inwazji, rozwój normalny), 3) u. przygodny (mała ekstensywność i intensywność inwazji, rozwój najczęściej zahamowany), 4) u. pozorny (przy małej ekstensywności i intensywności inwazji rozwój całkowicie zahamowany). Typy te pokrywają się częściowo z grupami żywicieli uprzednio wyróżnionymi (u. właściwy odpowiada grupie V, u. pomocniczy — grupie IV, u. pozorny — grupie II). Jeśli chodzi o pasożyty jelitowe (np. *Astasia cyclopis* w *Copepoda*) mogą kształtować się układy właściwy, pomocniczy i być może — przygodny, gdyż występuje jedna tylko bariera selekcyjna. Brak ostrych granic pomiędzy układami oraz ich zmienność, zależna od właściwości indywidualnych żywicieli i pasożytów, intensywności inwazji jak również czynników środowiska i pór roku, wskazują, że układy jako swoiste jednostki biologiczne mogą podlegać działaniu doboru naturalnego. Być może wymienione typy układów znajdą szersze zastosowanie w parazytologii, trzeba jednak pamiętać, że charakter układu „żywiciel-pasożyt" zależy od dróg inwazji, lokalizacji pasożyta w żywicielu, rejonu geograficznego (G u t t o w a, 1957). Proponowane jednolite metodyczne założenia badań terenowych i eksperymentalnych oraz ujmowania ich wniosków ilustrują przykładowo odpowiednie tabele.